ANTS AND SOME OTHER INSECTS.[1]

AN INQUIRY INTO THE PSYCHIC POWERS OF THESE ANIMALS, WITH AN APPENDIX ON THE PECULIARITIES OF THEIR OLFACTORY SENSE.

[CONCLUDED.]

THE REALM OF FEELING.

IT may perhaps sound ludicrous to speak of feelings in insects. But when we stop to consider how profoundly instinctive and fixed is our human life of feeling, how pronounced are the emotions in our domestic animals, and how closely interwoven with the impulses, we should expect to encounter emotions and feelings in animal psychology. And these may indeed be recognised so clearly that even Uexkuell would have to capitulate if he should come to know them more accurately. We find them already interwoven with the will as we have described it. Most of the emotions of insects are profoundly united to the instincts. Of such a nature is the jealousy of the queen bee when she kills the rival princesses, and the terror of the latter while they are still within their cells; such is the rage of fighting ants, wasps, and bees, the above-mentioned discouragement, the love of the brood, the self-devotion of the worker honey-bees, when they die of hunger while feeding their queen, and many other cases of a similar description. But there are also individual emotions that are not compelled altogether by instinct, e. g., the above-mentioned mania of certain ants for maltreating some of their antagonists. On the other hand, as I have

[1] Lectures delivered in Berlin, August 13, 1901, before the Fifth International Congress of Zoölogists. Published by Ernst Reinhard, Munich, 1901. Translated from the German by William Morton Wheeler.

shown, friendly services (feeding), under exceptional circumstances, may call forth feelings of sympathy and finally of partnership, even between ants of differents species. Further than this, feelings of sympathy, antipathy, and anger among ants may be intensified by repetition and by the corresponding activities, just as in other animals and man.

The social sense of duty is instinctive in ants, though they exhibit great individual, temporary, and occasional deviations, which betray a certain amount of plasticity.

PSYCHIC CORRELATIONS.

I have rapidly reviewed the three main realms of ant-psychology. It is self-evident that in this matter they no more admit of sharp demarcation from one another than elsewhere. The will consists of centrifugal resultants of sense-impressions and feelings and in turn reacts powerfully on both of these.

It is of considerable interest to observe the antagonism between different perceptions, feelings, and volitions in ants and bees, and the manner in which in these animals the intensely fixed (obsessional) attention may be finally diverted from one thing to another. Here experiment is able to teach us much. While bees are busy foraging on only one species of flower, they overlook everything else, even other flowers. If their attention is diverted by honey offered them directly, although previously overlooked, they have eyes only for the honey. An intense emotion, like the swarming of honey-bees (von Buttel) compells these insects to forget all animosities and even the old maternal hive to which they no longer return. But if the latter happens to be painted blue, and if the swarming is interrupted by taking away the queen, the bees recollect the blue color of their old hive and fly to hives that are painted blue. Two feelings often struggle with each other in bees that are "crying" and without a queen: that of animosity towards strange bees and the desire for a queen. Now if they be given a strange queen by artificial means, they kill or maltreat her, because the former feeling at first predominates. For this reason the apiarist encloses the strange queen in a wire cage. Then the

foreign odor annoys the bees less because it is further away and they are unable to persecute the queen. Still they recognise the specific queen-odor and are able to feed her through the bars of the cage. This suffices to pacify the hive. Then the second feeling quickly comes to the front; the workers become rapidly inured to the new odor and after three or four days have elapsed, the queen may be liberated without peril.

It is possible in ants to make the love of sweets struggle with the sense of duty, when enemies are made to attack a colony and honey is placed before the ants streaming forth to defend their nest. I have done this with *Formica pratensis*. At first the ants partook of the honey, but only for an instant. The sense of duty conquered and all of them without exception, hurried forth to battle and most of them to death. In this case a higher decision of instinct was victorious over the lower impulse.

In *résumé* I would lay stress on the following general conclusions:

1. From the standpoint of natural science we are bound to hold fast to the psychophysiological theory of identity (Monism) in contradistinction to dualism, because it alone is in harmony with the facts and with the law of the conservation of energy.

Our mind must be studied simultaneously both directly from within and indirectly from without, through biology and the conditions of its origin. Hence there is such a thing as comparative psychology of other individuals in addition to that of self, and in like manner we are led to a psychology of animals. Inference from analogy, applied with caution, is not only permissible in this science, but obligatory.

2. The senses of insects are our own. Only the auditory sense still remains doubtful, so far as its location and interpretation are concerned. A sixth sense has not yet been shown to exist, and a special sense of direction and orientation is certainly lacking. The vestibular apparatus of vertebrates is merely an organ of equilibration and mediates internal sensations of acceleration, but gives no orientation in space outside of the body. On the other hand the visual and olfactory senses of insects present varieties in the range

of their competency and in their specific energies (vision of ultra-violet, functional peculiarities of the facetted eye, topochemical antennal sense and contact-odor).

3. Reflexes, instincts, and plastic, individually adaptive, central nervous activities pass over into one another by gradations. Higher complications of these central or psychic functions correspond to a more complicated apparatus of superordinated neuron-complexes (cerebrum).

4. Without becoming antagonistic, the central nervous activity in the different groups and species of animals complicates itself in two directions: (*a*) through inheritance (natural selection, etc.) of the complex, purposeful automatisms, or instincts; (*b*) through the increasingly manifold possibilities of plastic, individually adaptive activities, in combination with the faculty of gradually developing secondary individual automatisms (habits).

The latter mode requires many more nerve-elements. Through heredity predispositions (imperfect instincts) of greater or less stability, it presents transitions to the former mode.

5. In social insects the correlation of more developed psychic powers with the volume of the brain may be directly observed.

6. In these animals it is possible to demonstrate the existence of memory, associations of sensory images, perceptions, attention, habits, simple powers of inference from analogy, the utilisation of individual experiences and hence distinct, though feeble, plastic, individual deliberations or adaptations.

7. It is also possible to detect a corresponding, simpler form of volition, i. e., the carrying out of individual decisions in a more or less protracted time-sequence, through different concatenations of instincts; furthermore different kinds of discomfort and pleasure emotions, as well as interactions and antagonisms between these diverse psychic powers.

8. In insect behavior the activity of the attention is one-sided and occupies a prominent place. It narrows the scope of behavior and renders the animal temporarily blind (inattentive) to other sense-impressions.

Thus, however different may be the development of the auto-

matic and plastic, central neurocyme activities in the brains of different animals, it is surely possible, nevertheless, to recognise certain generally valid series of phenomena and their fundamental laws.

Even to-day I am compelled to uphold the seventh thesis which I established in 1877 in my habilitation as *privat-docent* in the University of Munich:

"All the properties of the human mind may be derived from the properties of the animal mind."

I would merely add to this:

"And all the mental attributes of higher animals may be derived from those of lower animals." In other words: The doctrine of evolution is quite as valid in the province of psychology as it is in all the other provinces of organic life. Notwithstanding all the differences presented by animal organisms and the conditions of their existence, the psychic functions of the nerve-elements seem nevertheless, everywhere to be in accord with certain fundamental laws, even in the cases where this would be least expected on account of the magnitude of the differences.

APPENDIX.

THE PECULIARITIES OF THE OLFACTORY SENSE IN INSECTS.

Our sense of smell, like our sense of taste, is a chemical sense. But while the latter reacts only to substances dissolved in liquids and with but few (about five) different principal qualities, the olfactory sense reacts with innumerable qualities to particles of the most diverse substances dissolved in the atmosphere. Even to our relatively degenerate human olfactories, the number of these odor-qualities seems to be almost infinite.

In insects that live in the air and on the earth the sense of taste seems to be located, not only like our own, in the mouth-parts, but also to exhibit the same qualities and the corresponding reactions. At any rate it is easy to show that these animals are usually very fond of sweet, and dislike bitter things, and that they perceive these two properties only after having tasted of the re-

spective substances. F. Will, in particular, has published good experiments on this subject.

In aquatic insects the conditions are more complicated. Nagel, who studied them more closely, shows how difficult it is in these cases to distinguish smell from taste, since substances dissolved in water are more or less clearly perceived or discerned from a distance by both senses and sought or avoided in consequence. Nagel, at any rate, succeeded in showing that the palpi, which are of less importance in terrestrial insects, have an important function in aquatic forms.

In this place we are concerned with an investigation of the sense of smell in terrestrial insects. Its seat has been proved to be in the antennæ. A less important adjunct to these organs is located, as Nagel and Wasmann have shown, in the palpi. In the antennæ it is usually the club or foliaceous or otherwise formed dilatations which accommodate the cellular ganglion of the antennary nerve. I shall not discuss the histological structure of the nerve-terminations but refer instead to Hicks, Leydig, Hauser, my own investigations and the other pertinent literature, especially to K. Kraepelin's excellent work. I would merely emphasise the following points:

1. All the olfactory papillæ of the antennæ are transformed, hair-like pore-canals.

2. All of these present a cellular dilatation just in front of the nerve-termination.

3. Tactile hairs are found on the antennæ together with the olfactory papillæ.

4. The character and form of the nerve-terminations is highly variable, but they may be reduced to three principal types: pore-plates, olfactory rods, and olfactory hairs. The two latter are often nearly or quite indistinguishable from each other. The nerve-termination is always covered with a cuticula which may be never so delicate.

Other end-organs of the Hymenopteran antenna described by Hicks and myself, are still entirely obscure, so far as their function is concerned, but they can have nothing to do with the sense of

smell, since they are absent in insects with a delicate sense of smell (wasps) and accur in great numbers in the honey-bees, which have obtuse olfactories.

That the antennæ and not the nerve-terminations of the mouth and palate functions are organs of smell, has been demonstrated by my control experiments, which leave absolutely no grounds for doubt and have, moreover, been corroborated on all sides. Terrestrial insects can discern chemical substances at a distance by means of their antennæ only. But in touch, too, these organs are most important and the palpi only to a subordinate extent, namely in mastication. The antennæ enable the insect to perceive the chemical nature of bodies and in particular, to recognise and distinguish plants, other animals and food, except in so far as the visual and gustatory senses are concerned in these activities. These two senses may be readily eliminated, however, since the latter functions only during feeding and the former can be removed by varnishing the eyes or by other means. Many insects, too, are blind and find their way about exclusively by means of their antennæ. This is the case, e. g., with many predatory ants of the genus Eciton.

But I will here assume these questions to be known and answered, nor will I indulge in polemics with Bethe and his associates concerning the propriety of designating the chemical antennal sense as "smell." I have discussed this matter elsewhere.[1] What I wish to investigate in this place is the psychological quality of the antennal olfactory sense, how it results in part from observation and in part from the too little heeded correlative laws of the psychological exploitation of each sense in accordance with its structure. I assume as known the doctrines of specific energies and adequate stimuli, together with the more recent investigations on the still undifferentiated senses, like photodermatism and the like, and would refer, moreover, to Helmholtz's *Die Thatsachen in der Wahrnehmung*, 1879. Hirschwald, Berlin.

---

[1] "Sensations des Insects," *Rivista di Biologia Generale*. Como, 1900–1901. For the remainder see also A. Forel, *Mitth. des Münchener entom. Vereins*, 1878, and *Recueil. Zool. Suisse*, 1886–1887.

When in our own human subjective psychology, which alone is known to us directly, we investigate the manner in which we interpret our sensations, we happen upon a peculiar fact to which especially Herbert Spencer has called attention. We find that so-called perceptions consist, as is well known, of sensations which are bound together sometimes firmly, sometimes more loosely. The more intimately the sensations are bound together to form a whole, the easier it is for us to recall in our memory the whole from a part. Thus, e. g., it is easy for me to form an idea from the thought of the head of an acquaintance as to the remainder of his body. In the same manner the first note of a melody or the first verse of a poem brings back the remainder of either. But the thought of an odor of violets, a sensation of hunger, or a stomach-ache, are incapable of recalling in me either simultaneous or subsequent odors or feelings.

These latter conditions call up in my consciousness much more easily certain associated visual, tactile, or auditory images (e. g., the visual image of a violet, a table set for a meal). As ideas they are commonly to be represented in consciousness only with considerable difficulty, and sometimes not at all, and they are scarcely capable of association among themselves. We readily observe, moreover, that visual images furnish us mainly with space recollections, auditory images with sequences in time, and tactile images with both, but less perfectly. These are indubitable and well-known facts.

But when we seek for the wherefore of these phenomena, we find the answer in the structure of the particular sense-organ and in its manner of functioning.

It is well known that the eye gives us a very accurate image of the external world on our retina. Colors and forms are there depicted in the most delicate detail, and both the convergence of our two eyes and their movement and accommodation gives us besides the dimensions of depth through stereoscopic vision. Whatever may be still lacking or disturbing is supplied by instinctive inferences acquired by practice, both in memory and direct perception (like the lacunæ of the visual field), or ignored (like the

turbidity of the corpus vitreum). But the basis of the visual image is given in the coördinated *tout ensemble* of the retinal stimuli, namely the retinal image.[1] Hence, since the retina furnishes us with such spatial projections, and these in sharp details, or relations, definitely coördinated with one another, the sense of sight gives us knowledge of space. For this reason, also, and solely on this account, we find it so easy to supply through memory by association the missing remnant of a visual spatial image. For this reason, too, the visual sensations are preëminently associative or relational in space, to use Spencer's expression. For the same reason the insane person so readily exhibits halucinations of complicated spatial images in the visual sphere. This would be impossible in the case of the olfactory sense.

Similarly, the organ of Corti in the ear gives us tone or sound scales in accurate time-sequence, and hence also associations of sequence much more perfectly than the other senses. Its associations are thus in the main associations of sequence, because the end-apparatus registers time-sequences in time-intervals and not as space images.

The corresponding cortical receptive areas are capable, in the first instance, merely of registering what is brought to them by the sense-stimuli and these are mainly associated spatial images for sight and tone or sound-sequences for hearing.

Let us consider for a moment how odors strike the mucous membranes of our choanæ. They are wafted towards us as wild mixtures in an airy maelstrom, which brings them to the olfactory terminations without order in the inhaled air or in the mucous of the palate. They come in such a way that there cannot possibly be any spatial association of the different odors in definite relationships. In time they succeed one another slowly and without order, according to the law of the stronger element in the mixture, but

---

[1] It is well known that in this matter the movements of the eyes, the movements of the body and of external objects play an essential part, so that without these the eye would fail to give us any knowledge of space. But I need not discuss this further, since the antennæ of ants are at least quite as moveable and their olfactory sense is even more easily educated in unison with the tactile sense.

without any definite combination. If, after one has been inhaling the odor of violets, the atmosphere gradually becomes charged with more roast meat than violet particles, the odor of roast succeeds that of violet. But nowhere can we perceive anything like a definitely associated sequence, so that neither our ideas of time nor those of space comprise odors that revive one another through association. By much sniffing of the surface of objects we could at most finally succeed in forming a kind of spatial image, but this would be very difficult owing to man's upright posture. Nevertheless it is probable that dogs, hedge-hogs, and similar animals acquire a certain olfactory image by means of sniffing. The same conditions obtain in the sphere of taste and the visceral sensations for the same reasons. None of these senses furnish us with any sharply defined qualitative relations either in space or time. On this account they furnish by themselves no associations, no true perceptions, no memory images, but merely sensations, and these often as mixed sensations, which are vague and capable of being associated only with associative senses. The hallucinations of smell, taste, and of the splanchnic sensations, are not deceptive perceptions, since they cannot have a deceptive resemblance to objects. They are simply paræsthesias or hyperæsthesias, i. e., pathological sensations of an elementary character either without adequate stimulus or inadequate to the stimulus.

The tactile sense furnishes us with a gross perception of space and of definite relations, and may, therefore, give rise to hallucinations, or false perceptions of objects. By better training its associative powers in the blind may be intensified. The visual sensations are usually associated with tactile localisations.

Thus we see that there is a law according to which the psychology of a sense depends not only on its specific energy but also on the manner in which it is able to transmit to the brain the relations of its qualities in space and time. On this depends the knowledge we acquire concerning time and space relations through a particular sense and hence also its ability to form perceptions and associations in the brain. More or less experience is, of course, to be added or subtracted, but this is merely capable of enriching

the knowledge of its possessor according to the measure of the relations of the particular sense-stimuli in space and time.

I would beg you to hold fast to what I have said and then to picture to yourselves an olfactory sense, i. e., a chemical sense effective at a distance and like our sense of smell, capable of receiving impressions from particles of the most diverse substances diffused through the atmosphere, located not in your nostrils, but on your hands. For of such a nature is the position of the olfactory sense on the antennal club of the ant.

Now imagine your olfactory hands in continual vibration, touching all objects to the right and to the left as you walk along, thereby rapidly locating the position of all odoriferous objects as you approach or recede from them, and perceiving the surfaces both simultaneously and successively as parts of objects differing in odor and position. It is clear from the very outset that such sense-organs would enable you to construct a veritable odor-chart of the path you had traversed and one of double significance:

1. A clear contact-odor chart, restricted, to be sure, to the immediate environment and giving the accurate odor-form of the objects touched (round odors, rectangular odors, elongate odors, etc.) and further hard and soft odors in combination with the tactile sensations.

2. A less definite chart which, however, has orienting value for a certain distance, and produces emanations which we may picture to ourselves like the red gas of bromine which we can actually see.

If we have demonstrated that ants perceive chemical qualities through their antennæ both from contact and from a distance, then the antennæ must give them knowledge of space, if the above formulated law is true, and concerning this there can be little doubt. This must be true even from the fact that the two antennæ simultaneously perceive different and differently odoriferous portions of space.[1]

[1] It is not without interest to compare these facts with Condillac's discussion (*Treatise on the Sensations*) concerning his hypothetical statue. Condillac shows that our sense of small is of itself incapable of giving us space knowledge. But it

They must therefore also transmit perceptions and topographically associated memories concerning a path thus touched and smelled. Both the trail of the ants themselves and the surrounding objects must leave in their brains a chemical (odor-) space-form with different, more or less definitely circumscribed qualities, i. e., an odor-image of immediate space, and this must render associated memories possible. Thus an ant must perceive the forms of its trail by means of smell. This is impossible, at least for the majority of the species, by means of the eyes. If this is true, an ant will always be able, no matter where she may be placed on her trail, to perceive what is to the right, left, behind or before her, and consequently what direction she is to take, according to whether she is bound for home, or in the opposite direction to a tree infested with Aphides, or the like.

Singularly enough, I had established this latter fact in my "Études Myrmeoologiques en 1886" (*Annales de la Societé Entomologique de Belgique*) before I had arrived at its theoretical interpretation. But I was at once led by this discovery in the same work to the interpretation just given. Without knowing of my work in this connection, A. Bethe has recently established (discovered, as he supposes) this same fact, and has designated it as "polarisation of the ant-trail." He regards this as the expression of a mysterious, inexplicable force, or polarisation. As we have seen, the matter is not only no enigma, but on the contrary, a necessary psychological postulate. We should rather find the absence of this faculty incomprehensible.

But everything I have just said presupposes a receptive brain. The formation of lasting perceptions and associations cannot take place without an organ capable of fixing the sense-impressions and of combining them among themselves. Experience shows that the immediate sensory centers are inadequate to the performance of this task. Though undoubtedly receptive, they are, nevertheless, incapable of utilising what has been received in the development

---

is different in the case of the topochemical sense of smell in combination with the antennary movements. Here Condillac's conditions of the gustatory sense are fulfilled.

of more complex instincts and can turn it to account only in the grosser, simpler reflexes and automatisms. To be sure, a male ant has better eyes than a worker ant, and probably quite as good antennæ, but he is unable to remember that he has seen and is especially incapable of associating it in the form of a trail-image, because he is almost devoid of a brain. For this reason he is unable to find his way back to the nest. On the other hand, it is well known that the brain of a man who has lost a limb or whose hearing is defective, will enable him to paint pictures with his foot, write with the stump of an arm or construct grand combinations from the images of defective senses.

I venture, therefore, to designate as topochemical the olfactory antennal sense of honey-bees, humble-bees, wasps, etc.

Can we generalise to such an extent as to apply this term without further investigation to all arthropods. To a considerable extent this must be denied.

In fact the multiformity in the structure and development of the arthropod sense-organs is enormous, and we must exercise caution in making premature generalisations.

It is certain that in some aerial insects the olfactory sense has dwindled to a minimum, e. g., in those species in which the male recognises and follows the female exclusively by means of the eyes, as in the Odonata (dragon-flies). To insects with such habits an olfactory sense would be almost superfluous. Here, too, the antennæ have dwindled to diminutive dimensions.

But there are insects whose antennæ are immovable and quite unable to touch objects. This is the case in most Diptera (flies). Still these antennæ are often highly developed and present striking dilatations densely beset with olfactory papillæ. By experiment I have demonstrated the existence of an olfactory sense in such Dipteran antennæ, and I have been able to show that, e. g., in *Sarcophaga vivipara* and other carrion flies, the egg-laying instinct is absolutely dependent on the sensation of the odor of carrion and the presence of the antennæ. In these cases the contact-odor sense is undoubtedly absent. More or less of a topochemical odor-sense at long range must, of course, be present, since the antennæ are

external, but the precision of the spatial image must be very imperfect, owing to the immobility of the antennæ. Nevertheless, flies move about so rapidly in the air that they must be able by means of their antennæ to distinguish very quickly the direction from which odors are being wafted. These insects do, in fact, find the concealed source of odors with great assurance. But this is no great art, for even we ourselves are able to do the same by sniffing or going to and fro. But the flies find their way through the air with their eyes and not at all by means of their sense of smell. Hence their olfactory powers probably constitute a closer psychoogical approximation to those of mammals than to the topochemical odor-sense of ants, for they can hardly furnish any constant and definite space-relations.

Even in many insects with movable antennæ and of less ærial habits, e. g., the chafers and bombycid moths, the antennal olfactory sense is evidently much better adapted to function at a distance, i. e., to the perception of odors from distant objects, than to the perception of space and trails. Such insects find their way by means of their eyes, but fly in the direction whence their antennæ perceive an odor that is being sought.

A genuine topochemical antennal sense is, therefore, probably best developed in all arthropods, whose antennæ are not only movable in the atmosphere, but adapted to feeling of objects. In these cases the still imperfect topochemical oder-sense for distances can be momentarily controlled by the contact-odor-sense and definitively fixed topographically, i. e., topochemically, as we see so extensively practised in the ants.

It would be possible to meet this view with the objection that a contact-odor sense could not accomplish much more than the tactile sense. I have made this objection to myself. But in the first place it is necessary to reckon with the facts. Now it is a fact that insects in touching objects with their antennæ mainly perceive and distinguish the chemical constitution of the objects touched and heed these very much more than they do the mechanical impacts also perceived at the same time. Secondly, the tactile sense gives only resistance and through this, form. On the other hand,

the multiplicity of odors is enormous, and it is possible to demonstrate, as I have done for the ants, and Von Buttel-Reepen for the bees, that these animals in distinguishing their different nest-mates and their enemies, betray nothing beyond the perception of extremely delicate and numerous gradations in the qualities of odors.

In combination with topochemical space-perception, these numerous odor-qualities must constitute a spatial sense which is vastly superior to the tactile sense. The whole biology of the social Hymenoptera furnishes the objective proof of this assertion.

It would certainly be well worth while to investigate this matter in other groups of arthropods which possess complex instincts.

In conclusion I will cite an example, which I have myself observed, for the purpose of illustrating the capacity of the topochemical olfactory sense.

The American genus Eciton comprises predatory ants that build temporary nests from which they undertake expeditions for the purpose of preying on all kinds of insects. The Ecitons follow one another in files, like geese, and are very quick to detect new hunting grounds. As "ants of visitation," like the Africo-Indian species of Dorylus, they often take possession of human dwellings, ferret about in all the crevices of the walls and rooms for spiders, roaches, mice, and even rats, attack and tear to pieces all such vermin in the course of a few hours and then carry the booty home. They can convert a mouse into a clean skeleton. They also attack other ants and plunder their nests.

Now all the workers of the African species of Dorylus and of many of the species of Eciton are totally blind, so that they must orient themselves exclusively by means of their antennal sense.

In 1899 at Faisons, North Carolina, I was fortunate enough to find a temporary nest of the totally blind little *Eciton carolinense* in a rotten log. I placed the ants in a bag and made them the subject of some observations. The Eciton workers carry their elongate larvæ in their jaws and extending back between their legs in such a position that the antennæ have full play in front.

Their ability to follow one another and to find their way about rapidly and unanimously in new territory without a single ant go-

ing astray, is incredible. I threw a handful of Ecitons with their young into a strange garden in Washington, i. e., after a long railway journey and far away from their nest. Without losing a moment's time, the little animals began to form in files which were fully organised in five minutes. Tapping the ground continually with their antennæ, they took up their larvæ and moved away in order, reconnoitering the territory in all directions. Not a pebble, not a crevice, not a plant was left unnoticed or overlooked. The place best suited for concealing their young was very soon found, whereas most of our European ants under such conditions, i. e., in a completely unknown locality, would probably have consumed at least an hour in accomplishing the same result. The order and dispatch with which such a procession is formed in the midst of a totally strange locality is almost fabulous. I repeated the experiment in two localities, both times with the same result. The antennæ of the Ecitons are highly developed, and it is obvious that their brain is instinctively adapted to such rapid orientation in strange places.

In Columbia, to be sure, I had had opportunities of observing, not the temporary nests, but the predatory expeditions of larger Ecitons (*E. Burchelli* and *hamatum*) possessing eyes. But these in no respect surpassed the completely blind *E. carolinense* in their power of orientation and of keeping together in files. As soon as an ant perceives that she is not being followed, she turns back and follows the others. But the marvellous fact is the certainty of this recognition, the quickness and readiness with which the animals recognise their topochemical trail without hesitation. There is none of the groping about and wandering to and fro exhibited by most of our ants. Our species of Tapinoma and Polyergus alone exhibit a similar but less perfect condition. It is especially interesting, however, to watch the *perpetuum mobile* of the antennæ of the Ecitons, the lively manner in which these are kept titillating the earth, all objects, and their companions.

All this could never be accomplished by a tactile sense alone. Nor could it be brought about by an olfactory sense which furnished no spatial associations. As soon as an Eciton is deprived of its

two antennæ it is utterly lost, like any other ant under the same circumstances. It is absolutely unable to orient itself further or to recognise its companions.

In combination with the powerful development of the cerebrum (*corpora pedunculata*) the topochemical olfactory sense of the antennæ constitutes the key to ant psychology. Feeling obliged to treat of the latter in the preceeding lecture, I found it necersary here to discuss in detail this particular matter which is so often misunderstood.[1]

---

[1] In his latest *Souvenirs entomologiques* (Seventh Series) J. H. Fabre has recorded a number of ingenious experiments showing the ability of the males of Saturnia and Bombyx to find their females at great distances and in concealment. He tried in vain (which was to have been foreseen) to conceal the female by odors which are strong even to our olfactories. The males came notwithstanding. He established the following facts: (1) Even an adverse wind does not prevent the males from finding their way; (2) if the box containing the female is loosely closed, the males come nevertheless; (3) if it is hermetically closed (e. g., with wadding or soldered) they no longer come; (4) the female must have settled for some time on a particular spot before the males come; (5) if the female is then suddenly placed under a wire netting or a bell-jar, though still clearly visible, *the males nevertheless do not fly to her, but pass on to the spot where she had previously rested and left her odor*; (6) the experiment of cutting off the antennæ proves very little. The males without antennæ do not, of course, come again; but even the other males usually come only once: their lives are too short and too soon exhausted.

At first Fabre did not wish to believe in smell, but he was compelled finally, as a result of his own experiments, to eliminate sight and hearing. Now he makes a bold hypothesis: the olfactory sense of insects has two energies, one (ours), which reacts to dissolved chemical particles, and another which receives "physical odor-waves," similar to the waves of light and sound. He already foresees how science will provide us with a "radiography of odors" (after the pattern of the Roentgen rays). But his own results, enumerated above under (4) and (5) contradict this view. The great distances from which the Bombyx males can discern their females is a proof to him that this cannot be due to dissolved chemical particles. And these same animals smell the female only after a certain time and smell the spot where she had rested, instead of the female when she is taken away! This, however, would be inconceivable on the theory of a physical wave-sense, while it agrees very well with that of an extremely delicate, chemical olfactory sense.

It is a fact that insects very frequently fail to notice odors which we perceive as intense, and even while these are present, detect odors which are imperceptible to our olfactories. We must explain this as due to the fact that the olfactory papillæ of different species of animals are especially adapted to perceiving very different substances. All biological observations favor this view, and our psycho-chemical theories will have to make due allowance for the fact.

ZURICH, SWITZERLAND. AUGUST FOREL.